

CHEMOSYSTEMATIC DATA: THEIR USE IN THE STUDY OF DISJUNCTIONS¹

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Cain (1944) in his excellent text, *Foundations of Plant Geography*, does not use the term disjunct to describe those taxa having discontinuous distributions; rather, he uses the term vicariads (sometimes spelled vicariants), which he defines as "closely related allopatric species derived from a common ancestral population." Closely related allopatric species are usually only peripherally allopatric and hence are not the same as the term disjunct as used in this paper. Other workers, however, such as Setchell (1935) have defined vicariads as any two species only slightly discontinuous morphologically but widely discontinuous geographically. This, of course, is the meaning which most of the present contributors assign to the term disjunction. However, as indicated by Good (1953) the term vicariad has been loosely applied to almost any pair of related taxa showing almost any degree of disjunction. Löve (1954) refers to disjunct taxa as corresponding taxa, using this term to cover all vicariads with unknown origins.

Disjunctions or discontinuous distributions (the term used by both Cain, 1944, and Good, 1953) may refer to the spatial conditions holding for taxa at any hierarchical level; thus one may speak of disjunctions at the varietal or specific level or at the generic level or higher. Because of the lax use of these terms and the fact that *all* populations and/or taxonomic categories possess some degree of discontinuity with respect to their aerial distribution, I would like to define disjuncts yet further in this particular contribution. Distinction, however, should be made between at least two kinds of disjuncts, depending upon the origin and phyletic status of the populations concerned.

Heretofore, plant geographers have mainly been responsible for the terminology pertaining to disjuncts, and many bizarre explanations have been given for their occurrence (*e.g.* Croizat, 1952). Most workers have been content, however, to merely catalog or describe their occurrence, with only brief schriфт given to their probable origins. This perhaps reflects the obvious difficulty in assembling any data other than the geographical and morphological, although much interesting work bearing on disjuncts has been proposed from cytogenetical data (Löve, 1954).

In any case, I am of the opinion that the terms autojuncts and allojuncts (proposed below) will prove useful in future efforts to communicate on this subject.

¹ I am grateful to Professor James Hanover of Michigan State University for personally providing plates from his interesting work with *Picea glauca* and to my colleague Professor Robert Flake for providing me with unpublished data regarding the clustering of disjunct populations within that species. Special gratitude is due my graduate student, Mr. Stewart Sanderson, who made available to me preliminary results of his most interesting work on *Hymenoxys odorata* and *H. anthemoides*. Parts of the original research referred to in this paper were supported by grants (GB-5548X) from the National Science Foundation.

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Further, use of these terms should suggest to the interested worker that some effort should be extended in determining the likely origin of a given disjunct, and *this* I believe will inevitably involve the worker with chemosystematic approaches to the problem. At least, chemical methods provide a large spectrum of new approaches to such problems, especially where convergent evolution has obscured what appears to be relatively simple cases of autojunction (*e.g.* with *Larrea divaricata*, as discussed below).

KINDS OF DISJUNCT POPULATIONS

Autodisjunctions (autojuncts): These may be defined as two or more morphologically similar populations that are widely separated spatially, the more remote elements having become isolated through the dissemination of appropriate colonizers from some *extant* population or gene pool. Except for those very few cases which have been studied in great detail, most autojuncts will of necessity be at the species level or below, that is to say the isolated population will be very similar to the parental population and is likely to be treated as a species by most taxonomists. Autojuncts may arise in a number of ways (see below), but most, very remote, populations of the same species are likely to have arisen through long distance dispersal from some much larger parental population. Where formidable barriers to the migration of species are lacking, autojuncts might arise as a result of the distributional expansion of a given population with subsequent regression so that the autojuncts are left as relict populations. The latter are likely to be quite similar to the more widespread parental populations. Given time, however, such autojuncts may diverge from the parental (extant) populations so that they may come to be recognized as subspecies or even closely related species. Lacking fossil data, however, convincing evidence for the wide morphological divergence of an autojunct from some extant populational source would be difficult to assemble.

Allodisjunctions (allojuncts): These may be defined as two or more closely related populations (*i.e.* more closely related to each other than either is to yet some other taxon) that are widely separated spatially, the various elements of which have been derived through phyletic divergence from populations now *extinct*. As indicated above, most allojuncts will be recognized in the first place by morphological criteria, the term being reasonably applicable to nearly all species, genera, families, etc., whose members have remote spatial disjunctions not explicable through origins from extant populations or taxa.

FORMATION OF DISJUNCTS

Disjunct populations or taxa are usually formed through any of the following:

- 1) long-range dispersal of seeds or propagules with the subsequent establishment of reproducing populations;
- 2) extinction of once intervening populations and subsequent survival (relict) of the more remote populational elements;
- 3) parallel divergence from ancestral populations, the latter becoming extinct;
- 4) "convergence" from phyletically remote populations;

- 5) remote isolation by purely tectonic forces (*e.g.* continental drift);
- 6) differential migration of whole populations following events, either physical or biological, leading to populational fragmentation.

If the parental populations or gene pool from which the original disjuncts arose persist, then disjunct populations might properly be referred to as autojuncts. This would be so whether or not the disjunct element diverged considerably or remained essentially like that of the parental population. Of course, the greater the genetic divergence of the disjunct populations from the more stabilized parental population, the more difficult it becomes to establish autojunction or allojunction, but it seems reasonable to assume that *most* cases involving 1) and 2) are likely autojunctional, while those involving 3) and 4) are allojunctional. Categories 5) and 6) may be either autojunctional or allojunctional depending upon the degree of adaptational divergence encountered in the gene pool following their initial isolation.

In any case, chemical data and their treatment by numerical methods already developed should make it possible to choose at least between some of these alternatives. Selected examples of the use of chemical data in such studies will be presented in the discussion that follows.

CHEMICAL APPROACHES IN THE STUDY OF DISJUNCTS

The study of disjuncts is essentially a systematic enterprise, and reasonable insight into the nature of such phenomena can only come as a result of detailed monographic study of the taxa involved. This would include the study of taxa related to, but not part of, the disjunct populations under consideration; consequently, if one contemplates the study of disjunct genera, he must consider the morphology and distribution of related genera; if at the species level, those species related to the disjuncts must be considered; and at the infraspecific level, a wide knowledge of the probably allojunct populations must be had, preferably from material drawn from throughout the range of both the parental population and its disjunctive body.

As indicated in previous reviews (Turner, 1967, 1969) chemical approaches to systematic problems can be broadly categorized as being either micromolecular or macromolecular. The latter involves work with very large molecules or polymeric compounds, while the former is concerned with compounds of small molecular weight, usually monomeric in nature.

Macromolecular approaches: There are four principal macromolecular approaches available for the study of disjuncts at the present time, these being 1) amino acid sequence analysis of proteins, 2) DNA/RNA hybridization, 3) serology, and 4) protein band and isozyme studies. The merits, shortcomings, and systematic potential of these various approaches have been considered in general detail elsewhere (Turner, 1967, 1969, 1971), and it need only be noted here that approaches 1), 2), and 3) are perhaps most applicable at the higher categorical levels while 4) is more applicable at the lower categorical levels.

Instrumental and technological advances are not available to permit the rapid acquisition of sufficient data from sequence analysis of proteins and DNA hybridi-

zation studies to make them especially useful in the study of disjuncts at present. The same may be said for serology, for the imposition of an antibody-producing organism in the methodological approach introduces serious constraints with respect to the breadth and number of samples which may be taken.

Protein-band and isozyme techniques, however, permit relatively rapid and extensive surveys among populations. In this respect, they are like micromolecular approaches, for a good technician using relatively simple procedures and instrumentation can accumulate considerable data of this sort. Unfortunately, there are serious problems in the interpretation of mere protein band data, especially when attempting to make comparative correlations among taxa at the species level or higher (Turner, 1967, 1969). Isozyme data are somewhat useful in that band homologies for comparative purposes can be reasonably assumed, but because of the considerable polymorphism found in most isozymes in natural plant populations (Marshall & Allard, 1970; Scogin, 1968), their application to the study of disjuncts becomes difficult (in that extensive surveys are needed to establish even *statistical* estimates of the variability occurring).

Nevertheless, isozymes should prove most useful in determining the origin of what appear to be clear cases of autojunction. In fact, I suspect that most examples of relatively recent (say within the last 500 years), long-range dispersal will be best documented by this approach, for introduction of a single autogamous plant into a new habitat far removed from its parental source is not likely to build up, in such rapid order, a variable gene pool for isozymes such as is likely to be possessed by the parental population from which it arose. Thus, while the disjunct element might colonize its new habitat quite rapidly, it will not be able to concomitantly build up a store of gene variability without some considerable time factor. Of course, if the disjunct population arose through the establishment of *several* outcrossing individuals, then the population will have a much better base for the accumulation of variability at the various loci concerned, but not nearly so great a variability as might exist in the parental populations.

Micromolecular approaches: Micromolecular approaches involve the study of chemical components of relatively small molecular weight compounds such as flavonoids, terpenoids, alkaloids, free amino acids, etc. Normally, they do not occur as other than mono- or bi-molecular units, and consequently, they are readily isolated and structurally identified by relatively simple techniques and instrumentation (*i.e.* isolation by chromatography and identification by spectroscopy). Because of their ease in identification they are perhaps more useful in the study of disjunction than mere protein-band data, for the establishment of character homology in disjuncts is critical. Their use in systematics has been soundly criticized by several workers, especially where the investigators concerned have made sweeping taxonomic generalizations from data taken from only a few individuals or populations.

It has been pointed out also that micromolecular compounds are likely to be much more ubiquitous than is generally conceded, as indicated by Professor W. L. Fowden of London Univ. (personal communication), who has identified several previously unreported (indeed unsuspected!) compounds in commercial quantities of sugar beet syrup, simply by having access to exceptionally large samples from

industrial sources. That is, these compounds occurred in such small quantities that they could not be detected by ordinary procedures.

Finally, it should be noted that micromolecular components of any one class are limited in number. Further, some of the more common types occur across a wide spectrum of plant taxa. This has been adequately emphasized by Alston (1967), and because of this, I feel that the primary application of micromolecular data to the study of discontinuous distributions should be to those situations involving autojunction. There are rare instances, however, where these data might prove quite convincing in the establishment of allojunction, even those at the familial level or higher. Perhaps the best example of this type reported to date is that involving the yellow and red pigments of the betalain type found in the order *Chenopodiales* (discussed below).

The extensive application of micromolecular data to systematic problems across a wide spectrum of plant taxa can be said to have begun only in the late 1950's and early 1960's (Alston & Turner, 1963). Because of this, relatively few chemical studies have been directed toward the study of disjuncts. Chemosystematic investigations, however, as judged by the publication and research currently going on, now appear to be in an early stage of exponential growth, and unquestionably such studies will be applied to problems of disjunction with increasing frequency.

The remainder of this paper, then, will concern itself with the consideration of a few selected examples in which micromolecular data have contributed toward the solution of both allo- and autojunction. By their nature, allojuncts are difficult to detect, but as already indicated (Turner, 1971) micromolecular data can prove very incisive in the study of populational problems at the infraspecific level.

CHEMICAL STUDIES BEARING ON ALLOJUNCTS

Cactaceae—*Aizoaceae*: According to Vierhapper (1919), these two families are vicariads or allojuncts (in my terminology). They are both very large, distinct categories, the members of which are apparently more closely related one to the other than either is to yet another taxon. The *Aizoaceae* is predominantly succulent, occurring mostly in the arid regions of the Old World, especially South Africa. The *Cactaceae* likewise is predominantly succulent, occurring mostly in the arid regions of the New World. Vierhapper's suggestion as to their allojunct nature is most extraordinary considering that he proposed this at a time when many experts thought the families to belong to quite different orders, and without knowledge of the recent evidence bearing on continental drift, to say nothing of the chemical data of the betalain type discussed here.

The close relationship of the *Cactaceae* and *Aizoaceae* is now widely accepted by most phyletic taxonomists. Much of the convincing evidence for this relationship rests on the fact that both families possess betalain pigments, a group of nitrogenous micromolecules restricted to the *Chenopodiales* (Wohlpert & Mabry, 1968).

My own speculations regarding the origin of this pair of allojuncts are as follows: It is probable that the ancestral populations from which these two families arose occupied xeric or at least halophytic habitats of the Southern Hemi-

sphere, probably on the ancient continent of Gondwanaland, presumably where southwestern Africa and southeastern South America were once connected. Subsequent gradual drift of these continents isolated some fraction of this primordial population, the South American fraction developing into the Cactaceae, the Old World elements developing into the Aizoaceae. Ancestral prototypic members no longer exist, but both families have retained their red and yellow betalain pigments (neither possess pigments of the anthocyanin type), and both still possess their peculiar sieve tube plastids, which are found in all members of the Chenopodiales (and Caryophyllales) but are absent in other plant families (Behnke & Turner, 1971).

Equally interesting is the occurrence of betalains in the small xerophytic family Didieraceae, which is restricted to Madagascar. The phyletic position of this family was long in dispute, but the discovery of betalain pigments in this family has convinced most workers that it belongs to the Chenopodiales. It will be interesting to consider possible allojuncts with this family, for Madagascar is believed to have been contiguous with India (McElhinny & Luck, 1970), and it might prove fruitful to examine those betalain families centered in India or Australia as possible disjuncts.

The more temperate, mostly mesophytic, Caryophyllaceae, which is often placed within the betalain-containing order (Behnke & Turner, 1971), does not contain betalain but *does* contain the peculiar sieve tube plastids characteristic of that order. It appears, therefore, that the Caryophyllaceae is a parallel offshoot of the ancestral phyletic line leading to the Chenopodiales. Interestingly, the Caryophyllaceae is mostly Northern Hemisphere in its distribution, while the Chenopodiales is either centered in the Southern Hemisphere or else is highly adapted to saline habitats or xeric conditions. This is particularly true of the latter order in the Southern Hemisphere where the group presumably had its origin. This point is emphasized here, for plant geographers and especially ecologists have tended to ignore phyletic adaptational trends, at least within higher plant categories, as especially significant in their studies of plant communities and their origin.³

CHEMICAL STUDIES BEARING ON AUTOJUNCTS

In the case of disjuncts at the higher categorical level, their characterization as possible autojuncts will undoubtedly prove difficult if not impossible. At the

³ I refer specifically to the suggestions of Axelrod (1950) and others as to the time of origin of the warm desert communities on the various continents. To assign an age of only one million years or so for most extant deserts does injustice to the considerable floristic evidence available. For example, the Cactaceae, Aizoaceae, Didieraceae, and presumably most of the families of the Chenopodiales were probably already xerophytically disposed even before the development of forces leading to continental drift, or else these betalain-containing families would not so often dominate such habitats on these widely separated continents today. This is to say nothing of the obviously xerophytic families Fouquieriaceae, Koeberliniaceae, Krameriaceae, Welwitschiaceae, etc., which are desert groups without close peripheral mesophytic relatives. That is, these families have probably been a feature of the deserts in which they occur for many millions of years, or else one must assume that nature is selectively capricious in her destruction of the presumably more stable, mesic relatives from which they have had to arise; lacking this, one must assume a degree of adaptational divergence from some once closely related ancestor, the like of which baffles the imagination.

generic or familial level recognition will depend heavily upon amino acid sequence studies of proteins or else must await the development of more sophisticated methods for the study of nucleotide sequences in DNA. Until such a time, morphological features will probably continue to serve as the primary criteria for their recognition.

At the species level or below, the establishment of disjunct populations as autojunctal will probably rely quite heavily upon microchemical data, for it is difficult to believe that purely morphological data might do more than provide a model against which to test the chemical data. Of the various microchemical components which have been used for systematic purposes, the most common have been flavonoids and volatile oils. The former are relatively easy to isolate and identify, but since they are usually detected on a presence or absence basis only, they are not particularly useful in the study of disjuncts, especially in those cases which appear to be autojunctal.

Ideally, chemical characters used in the study of putative autojuncts should be

- 1) rapidly and easily surveyed for, preferably by tests on a single individual or plant part;

- 2) readily quantified, preferably by automatic methods;

- 3) under genetic control so that they might respond to adaptational changes under selective influences.

At present, the group of compounds which best fills all three criteria are those which are easily identified by gas liquid chromatography (GLC), for example, terpenes. In fact, using combined GLC-mass spectroscopy and appropriate computer methods, it is possible to identify and quantitate up to 100 volatile components within a 60 minute period. All of this is done by the hardware, of course, leaving little, if anything, to procedural bias, except for the collection of the specimens from which the compounds are obtained, that itself being a kind of intuitive bias since one cannot observe chemical constituents in the field.

Further, the information, once assembled, lends itself to appropriate algorithms which purport to do for the chemical data what the taxonomist does for the morphological, with the exception that use of the former permits the objective (numerical) presentation of data along with statistical tests as to significance (Flake, von Rudloff & Turner, 1969). This is not generally true for the morphological data, and as indicated above, this cannot be done with chemical compounds such as flavonoids where quantitation is not so readily obtained.

In my consideration of the examples that follow, I would like to emphasize that their selection has been due primarily to their heuristic value in presenting the potential of such techniques, or else they have been selected for their enigmatic nature, inquiry into which must require ultimately some knowledge of the volatile constituents of the plants themselves.

Autojunct populations in Picea glauca: Wilkinson *et al.* (1971) have studied in considerable detail the monoterpene composition from 16 localities of *Picea glauca* (White Spruce) in North America (Fig. 1). While the study was confined to the analysis of only nine monoterpenes from ten trees from any one locality, it is remarkable in that all of the trees sampled were taken from nature and grown

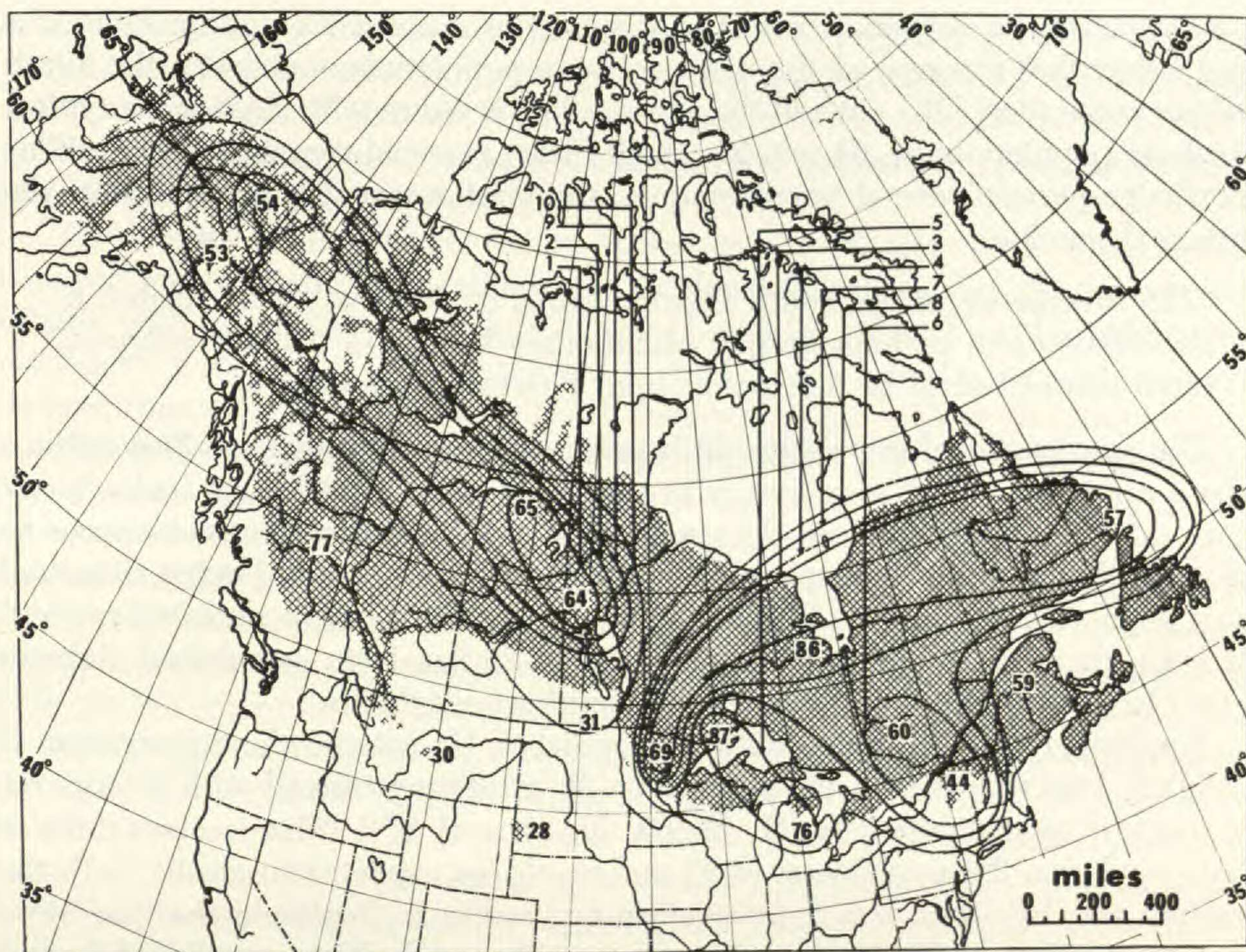


FIGURE 1. Aggregation contours of populations of white spruce (*Picea glauca*) using weighted chemical characters (Wilkinson *et al.*, 1971). The disjunct populations 30 and 28 clustered at a level below those for which contours are drawn and are discussed in more detail in the text.

in an experimental garden so that environmental factors affecting the variation were presumably minimal.

The study also pertains to this symposium, for it illustrates nicely the potential of chemical approaches to problems involving disjunction. *Picea glauca* exists in relatively extensive populations from northwestern North America to Alaska, south to the Great Lakes region of northern Minnesota and Illinois. There are, however, at least two well-defined disjunct populations, one in central Montana and the other in southwestern South Dakota. The latter, in particular, is isolated from the main populational mass by approximately 400 miles. Using replicated data and a character-weighting algorithm developed around the assumption that those characters showing the least variance from population to population ought to be given more weight in cluster analysis, Wilkinson *et al.* (1971) were able to show that the species consisted of two divergent chemical clines: one extending from the Lake States north-westward to Alaska, and the other north-eastward into Labrador. Furthermore, they suggested that these clines perhaps resulted from the migration of *P. glauca* both north-eastward and north-westward from populations to the south of the ice following glacial recession during post-Wisconsin time.

With knowledge of the chemical structure of the main populational mass, it was possible to consider the status of the disjunct populations 28 and 30 (Fig. 1).

It is interesting to note that these two populations entered the aggregations at a level below that for most of the more northern populations, but when the South Dakota population (28) entered the aggregation, it did so with a set of the typical "western" populations 54, 64, and 65 (R. H. Flake, personal communication). This knowledge permits several interpretations, the most reasonable being that of the authors themselves:

"The divergence of the South Dakota source could possibly be related to its isolation and perhaps unique evolutionary history in that the source is often considered to be a remnant from Pleistocene glaciation."

The autojunctional population 28 is presumably a relict stand of *Picea glauca* whose origin goes back to a time when the main populational mass had a much more extensive distribution to the south; that is, its isolation does not appear to relate to the more northern populations, the latter presumably having dispersed from populations arranged along the front of the most recently glaciated regions. At least, there is no evidence that population 28 has been established through recent long-range dispersal from its more northern neighbors.

Surprisingly, the Montana disjunct population 30 entered the aggregation at a slightly lower level than did population 28, clustering instead with a large set of "eastern" populations (44, 57, 60, 69, 76, 86, and 87)! This is anomalous in that population 30 is northwest of 28 and would be expected to cluster with the western set. However, this is believed to be readily explicable in that the Montana population occurs in a region of sympatry with *Picea engelmannii*, and chemical examination of populations in this area suggests that they are involved in hybridization (Habeck & Weaver, 1969). In short, the relationship of population 30 to the more eastern population seems to be spurious, resulting from peripheral perturbations in the gene pool of *P. glauca* as a result of hybridization with *P. engelmannii*. In fact, it was shown by Wilkinson *et al.* (1971) that hybridization between these two taxa should result in the kind of chemical variation actually found in the Montana population.

In my opinion, it would have been difficult, if not impossible, to assemble morphological evidence bearing on the origin of these two autojunctional populations without the use of chemical data. Differences among the various populations of *Picea glauca* are simply not sufficiently distinctive to permit any sort of objective structuring of the populations using morphological characters.

Hymenoxys odorata–*Hymenoxys anthemoides*: According to Parker (1962), these two species are thought to be disjuncts, *H. odorata* occurring in the desert regions of North America; *H. anthemoides* occurring in the drier regions of Argentina.

The genus *Hymenoxys* is centered in North America where two well-defined subgenera are recognized: *Hymenoxys* and *Tetraneuris*, some workers preferring to treat them as distinct genera. Both *H. odorata* and *H. anthemoides* belong to the subgenus *Hymenoxys*; the somewhat larger subgenus, *Tetraneuris*, is not represented in South America, while *Hymenoxys* is represented by four species.

The suggestion that *Hymenoxys anthemoides* is most closely related, on morphological grounds, to *H. odorata* is interesting because it bears upon the origin

of a whole group of interior arid land disjuncts with amphi-tropical distributions in the New World. In fact, this group of plants constitutes one of the most enigmatic assemblages of floristic disjunctions known to me, and there have been a number of hypotheses put forward to explain their occurrence (Bray, 1900; Johnston, 1940; Raven, this symposium).

The case for the disjunctive nature of *Hymenoxys odorata* and *H. anthemoides* received impetus with the preliminarily cytological findings that *H. odorata* was dibasic with chromosome numbers of $n = 11$ and 15 , while *H. anthemoides* was monobasic with $x = 15$. This suggested that the South America populations were derived from those populations in North America with $x = 15$ or vice versa.

This is about where the problem stood until about a year ago at which time Mr. Stewart Sanderson, graduate student at the University of Texas, began an intensive chemosystematic study of the subgenus *Hymenoxys* using terpenoid characters. His preliminary data bearing on the possible disjunctive nature of *Hymenoxys anthemoides* and *H. odorata* are quite interesting. The two species together possess over 40 volatile components, and examination of populations of both species grown in the same experimental garden has shown that only a few of these compounds are shared. In fact, by terpenoid chemistry, *H. anthemoides* is more closely related to some of the more restricted, mountainous species of North America than it is to *H. odorata*. Finally, the North American cytological races ($n = 11$ and 15) were clearly quite closely related by their terpenoid chemistry (and morphology), thereby denying any likely relationship between the races of *H. odorata* with $n = 15$ and *H. anthemoides* with $n = 15$.

Of course, the subgenus *Hymenoxys* must still be counted as a disjunctional element, but it seems clear from the chemical evidence available that the South American *H. anthemoides* is not particularly close to *H. odorata*, and the two species could scarcely be termed an autojunctional pair. A more likely explanation for their disjunction, if the taxonomic suggestions put forth by Parker are valid, is that they are allojuncts, the South American populations having reached the arid regions of the Southern Hemisphere via long-range dispersal at some distant time and that subsequent divergence of the North American parental population has occurred. The reason for asserting that North America is the ultimate place of origin for *Hymenoxys* is that this genus and related genera are far and away best developed on that continent (Bierner, 1971).

Other interpretations of these preliminary data are possible, of course, but it appears likely that a more comprehensive chemical study of the numerous species of *Hymenoxys* on both continents will do much to clarify the nature of these interesting disjuncts. In fact, taken together, a series of such studies on a wide spectrum of plant groups might do much to resolve the particular problem of whence came these amphi-tropical patterns and how. Indeed, such a collaborative study is already underway, and it will be most interesting to consider the impact of data assembled from these studies.

Larrea divaricata–*Larrea tridentata*: Of the numerous disjunct taxa worthy of chemosystematic study, the genus *Larrea* (Zygophyllaceae) seems unusually qualified for detailed investigation, since it is a dominant element of the desert vegetation in both North and South America; and at least one species, *L. divari-*

cata, is so similar to its southern hemisphere counterpart, *L. tridentata*, that some authors have considered them to be the same species. In fact, this is the best known example of an amphi-tropical autojunct. Since its distribution and ecological position in the deserts of both North America and South America are treated in detail by Solbrig (this symposium) and Hunziker *et al.* (this symposium), I will confine my remarks here to the potential contribution that comparative biochemistry might hold for the study of disjuncts.

On the surface, *Larrea* would seem to be an "ideal" genus to study chemosystematically. It possesses a large number of volatile compounds which are readily detected by gas chromatography. The plants occur in very large populations, and a single leafy branch will suffice for distillation purposes. Thus, one can sample individual shrubs over a large region, marking the plants with permanent tags so that re-samples might be made, if needed.

However, there are many problems, foremost of which is the quantitative variability likely to be induced in the volatile constituents by environmental factors. It has been amply demonstrated that the volatile fraction of a plant will vary significantly from month to month depending on the metabolic stage of the organism, which in turn presumably depends upon moisture and temperature conditions affecting the populational site itself. Much of this plant-to-plant variation can be "smoothed out" by statistical treatment of the populational data but, except for trees growing under conditions of reduced metabolism in the field (*e.g.* *Juniperus virginiana* and presumably other conifers which show little or no growth activity during the winter months; Flake, von Rudloff & Turner, 1969), chemical analyses should come from plants grown in a uniform garden. This is particularly important with a desert shrub such as *Larrea*, for preliminary work on field populations of *L. divaricata* has shown quite extraordinary quantitative variation from individual to individual at a given site, and from population to population, presumably depending upon the amount of ground water available to the plants. Such variation might be due to the extraordinary sensitivity of the volatile compounds themselves, most of which are guanilides, a group of peculiar constituents unrelated to the terpenes. Since *Larrea* is an evergreen shrub, more or less restricted to temperate regions, it might prove feasible to sample populations in the winter, much as in *Juniperus*, but this is an aspect of the problem which has not been investigated.

Finally, I cannot help but note that three views prevail as to the origin of the more xeric amphi-tropical elements found on the North and South American continents. These are:

- 1) that the species (and deserts) are ancient (60 million years or more) having a common origin;
- 2) that the floras evolved separately through parallel selective influences from the surrounding vegetation, *i.e.* the floras have no historical connections as such; or
- 3) that the species (and deserts) are of relatively recent origin, the disjuncts having reached the two desert areas via long-distance dispersal.

If the latter view (3) is held, then one would expect a very close similarity in the secondary compounds of the various disjunct taxa. On the other hand, if

very similar species have very different secondary compounds this might indicate a long-time isolation or different phyletic history of the taxa concerned, the morphological traits (*e.g.* habit and vegetative features), through parallel selective influences, remaining at least superficially similar; the secondary compounds, inasmuch as they are presumably under weak selective pressures probably reacted differently to the different parasitic and grazing fauna of the South American region. In other words the secondary compounds, being under quite different selective forces, should have diverged considerably from their disjunct counterparts in spite of the quite similar climatic regimes in which they presently occur (Turner, 1969).

As yet we do not know the origin of the apparently autojunct *Larrea divaricata*. Hunziker (personal communication, this symposium) interprets his preliminary protein-band data as suggestive of a South American origin for the group as a whole. I am more cautious, for while I recognize the better development of *Larrea* (as to number of species) in South America, I am also aware that the North American element is made up of diploid, tetraploid, and hexaploid populations, all of which show considerable variation, indicative of a species with some considerable tenure in the North American deserts. I suggest, therefore, that it is equally likely that *L. divaricata* developed as a diploid population in North America millions of years ago, and that subsequently it was established in South America through long-range dispersal. The fact that there are two other species of *Larrea* in South America implies little, for *L. divaricata* may be only remotely related to these. Of course, it is also possible that the genus itself, and *L. divaricata* specifically, has existed since early Tertiary time, such as suggested by Bray (1900) and Johnston (1940). But this would seem to raise serious problems as to the origin of the desert areas themselves, for it seems unlikely that the desert areas were ever connected such that *Larrea divaricata* achieved its disjunct status from a once intact gene pool with only subsequent physical events responsible for its isolation. Or does it?

I tend to believe that the disjuncts making up the various amphi-tropical elements have a multiplicity of origins. They may be allojunctional, as appears to be the case with *Hymenoxys odorata*-*H. anthemoides*, or they may be autojunctional, as appears to be the case with *Larrea divaricata*. Further, I tend to believe that the desert areas on the two continents developed early enough (at least beginning with Miocene) to have permitted the establishment of many kinds of disjuncts. Some of these are relatively old, and some relatively new, but presumably all have passed over the tropics as long-distance dispersants in one direction or the other.

Clearly, more data of every sort will be needed before these abominable amphi-tropical disjunctions can be explained or understood. No doubt comparative chemistry will make up an important part of this information.

LITERATURE CITED

- ALSTON, R. E. 1967. Biochemical Systematics. *Evol. Biol.* 1: 197-305.
——— & B. L. TURNER. 1963. Biochemical Systematics. Trenton, New Jersey.
AXELROD, D. I. 1950. Evolution of desert vegetation. *Publ. Carnegie Inst. Washington* 590: 215-306.

- BRAY, W. L. 1900. The relation of the North American flora to that of South America. *Science* 12: 709-716.
- BEHNKE, H.-D. & B. L. TURNER. 1971. On specific sieve-tube plastids in Caryophyllales. *Taxon* 20: 731-737.
- BIERNER, M. 1971. A chemosystematic and cytotaxonomic study of *Helenium*, sect. *Tetradus* (Compositae). Doctoral Dissertation, The University of Texas, Austin.
- CAIN, S. A. 1944. *Foundations of Plant Geography*. New York.
- CROIZAT, L. 1952. *Manual of Phyto-Geography*. The Hague.
- FLAKE, R. H., E. VON RUDLOFF & B. L. TURNER. 1969. Quantitative study of clinal variation in *Juniperus virginiana* using terpenoid data. *Proc. Natl. Acad. Sci. (U. S.)* 64: 487-494.
- GOOD, R. 1953. *The Geography of the Flowering Plants*. New York.
- HABECK, J. R. & T. W. WEAVER. 1969. A chemosystematic analysis of some hybrid spruce (*Picea*) populations in Montana. *Canad. Jour. Bot.* 47: 1565-1570.
- JOHNSTON, I. M. 1940. The floristic significance of shrubs common to North and South American deserts. *Jour. Arnold Arbor.* 21: 356-363.
- LÖVE, A. 1954. Cytotaxonomical evaluation of corresponding taxa. *Vegetatio* 5: 212-224.
- MARSHALL, D. R. & R. W. ALLARD. 1969. Genetic polymorphism in natural populations of *Avena fatua* and *A. barbata*. *Nature* 221: 276-278.
- McELHINNY, M. W. & G. R. LUCK. 1970. Paleomagnetism and Gondwanaland. *Science* 168: 830-832.
- PARKER, K. F. 1962. The South American species of *Hymenoxys* (Compositae). *Leaflet W. Bot.* 9: 197-209.
- SCOGIN, R. L. 1968. Isoenzyme polymorphism in selected enzymes in natural populations of the genus *Baptisia* (Leguminosae). Doctoral Dissertation, The University of Texas, Austin.
- SETCHELL, W. A. 1935. Pacific insular floras and Pacific paleogeography. *Amer. Naturalist* 69: 289-310.
- TURNER, B. L. 1967. Plant chemosystematics and phylogeny. *Jour. Pure Appl. Chem.* 14: 189-213.
- . 1969. Chemosystematics: recent developments. *Taxon* 18: 134-151.
- . 1971. Molecular approaches to populational problems at the infraspecific level. In "Phytochemical Phylogeny." London.
- VIERHAPPER, F. 1919. Über echten und falschen Vikarismus. *Oesterr. Bot. Zeitschr.* 68: 1-22.
- WILKINSON, R. C., J. W. HANOVER, J. W. WRIGHT & R. H. FLAKE. 1971. Genetic variation in the monoterpene composition of white spruce. *Forest Sci.* 17: 83-90.
- WOHLPART, A. & T. J. MABRY. 1968. The distribution and phylogenetic significance of the betalains with respect to the Centrospermae. *Taxon* 17: 148-152.